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# Studies on the Distribution of some Phthiracarid Mites (Acari: Oribatidae) in a Coniferous Forest Soil

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With one figure in the text

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## Contents

1.	Introduction . . . . .	252
2.	Methods . . . . .	253
3.	Results . . . . .	254
3.1.	Vertical Distribution . . . . .	254
3.2.	Degree of Aggregation . . . . .	255
3.3.	Transformation of the Raw Data . . . . .	256
3.4.	Horizontal Distribution . . . . .	256
3.4.1.	Spatial Distribution . . . . .	256
3.4.2.	Distribution under the Different Tree Species . . . . .	257
3.4.3.	Seasonal Changes . . . . .	258
4.	Discussion . . . . .	258
5.	Summary . . . . .	259
6.	Acknowledgements . . . . .	260
7.	References . . . . .	260

## 1. Introduction

The Phthiracaridae are a small family of Oribatid mites (Acari: Cryptostigmata), of which six genera and a dozen species have so far been recorded in Britain (TURK, 1953a, b) and all occur in soil or decaying organic material. Many workers have suggested that as the Phthiracaridae feed mainly on litter and decaying wood and have biting mouthparts, the members of this family play an important part in the decomposition of organic debris (JACOT, 1936, 1939; FORSSLUND, 1938; RIHA, 1951; SPENCER, 1951; SCHUSTER, 1955, 1956; WALLWORK, 1958; and DUNGER, 1958). Even though the members of this family occur commonly, particularly in coniferous forest soils, there have been no detailed investigations of their distribution in different habitats in Great Britain, although EVANS (1951) investigated the distribution of mites in a Sitka Spruce [*Picea sitchensis* (BONGARD) CARRIÈRE] plantation.

It was therefore decided to investigate the distribution of Phthiracarid mites in the soil of Coed Marian y Winllan, a small plantation of mixed coniferous species near Bangor (HAYES, 1962). This wood formerly comprised about 30 acres of old mixed hardwood approximately 100 to 150 years old, consisting mainly of *Quercus petraea* (MATTUSCHKA) LIEBL, *Fagus sylvatica* LINNÉ, and *Castanea sativa* MILL., with occasional trees of *Acer pseudoplatanus* LINNÉ, and *Betula verrucosa* EHRH. About thirty to thirty-five years ago, part of this wood was felled and replanted with conifers; *Abies grandis* LINDLEY,

*Larix decidua* MILLER, *Picea sitchensis* (BONGARD) CARRIÈRE, and *Pinus sylvestris* LINNÉ. The *Abies grandis* was planted as a small group, while the other species were planted either as small pure groups, or as a multiple line mixture with two or three lines of each species alternating.

There was no ground flora under the evergreen conifers, but under the hardwoods and to a lesser extent under the larch, there was a sparse ground flora which changed markedly with season.

### Ground flora recorded from Coed Marian y Winllan:

#### Angiospermae

<i>Deschampsia flexuosa</i> LINNÉ	<i>Digitalis purpurea</i> LINNÉ
<i>Endymion non-scripta</i> (LINNÉ) GARCKE	<i>Festuca rubra</i> LINNÉ
<i>Galium hercynicum</i> WEIG.	<i>Melandrium rubrum</i> (WEIG.) GARCKE
<i>Oxalis acetosella</i> LINNÉ	<i>Teucrium scorodonia</i> LINNÉ

#### Pteridophyta (Filicales)

*Dryopteris striata* (JACQ.) WAYNOR [= *D. dilatata* (HOFFM.) GRAY]

#### Bryophyta (Musci)

<i>Mnium hornum</i> LINNÉ	<i>Hypnum cupressiforme</i> LINNÉ
<i>Plagiothecium sylvaticum</i> B. et S.	<i>Polytrichum formosum</i> HEDW.
<i>Rhytidiadelphus loreus</i> (HEDW.) WARNST.	<i>Thuidium tamarascinum</i> B. et S.

#### Bryophyta (Hepaticae)

*Lophocolea* sp. [probably *L. bidentata* (LINNÉ) DUM.]

The nomenclature of the Angiospermae and Filicales is according to CLAPHAM, TUTIN and WARBURG (1952), and of the Musci and Hepaticae according to DIXON (1955) and WATSON (1955) respectively. The soil is a brown forest soil of low base status, and it is suggested that under the conifers, the soil is still in a transition stage from mixed hardwood mull to mor, since slight traces of leaching were observed in the upper soil horizons.

## 2. Methods

Since little detailed work on the distribution of the Phthiracarid mites in forest soils had been carried out, the opportunity was taken to use the samples collected by a colleague in Marian y Winllan during an investigation of the distribution of some other mite species. The sampling programme has already been reported (ATTALLA, 1961) and it is sufficient to note here the main points. The sampling was designed to collect evidence on the spatial distribution in relation to individual trees, with particular regard to the distance, depth and direction from the base of the stem. By sampling under trees of the genera *Abies*, *Larix*, *Picea* and *Pinus*, it was hoped to obtain information on the distribution of these mites in relation to tree species. Sampling was carried out at three monthly intervals over a period of 21 months.

Samples were taken in tubular stainless steel corers with a cross-sectional area of 10 sq. cm. and extracted on an apparatus designed and used by HOBART and POOLE (POOLE, 1957, 1961). This was based on the modified Tullgren funnel used by MACFADYEN (1953), but incorporated the split funnel principle of MURPHY (1955). The undisturbed cores were inverted when placed in the extraction apparatus so that the original upper surface of the sample was nearest to the collecting tube. Extraction was continued for one week and the animals were collected in tubes containing 70% alcohol. Counting was carried out under a binocular microscope using a magnification  $\times 35$ . It may be assumed that there is a high degree of reliability in the counting process, since the mites were relatively large, and it was not easy to overlook specimens left in the tubes or in the edges of the dishes used for counting.

The species found at Marian y Winllan and recorded in accordance with the nomenclature of WILLMANN (1931) were as follows:

- (1) *Hoplodermus magnum* (NICOLET, 1855) OUDEMANS, 1900 [= *Steganacarus magnus* NICOLET, 1855]
- (2) *Hoplodermus spinosus* (SELLNICK, 1920)
- (3) *Phthiracarus piger* (SCOPOLI, 1763)
- (4) *Oribotritia loricata* (RATHKE, 1799) [= *Pseudotritia ardua* KOCH, 1841]

### 3. Results

#### 3.1. Vertical Distribution

The first set of samples to determine vertical distribution was taken in January 1960. At each sampling point the litter and humus were collected in separate corers, and the top three inches (76 mm.) of soil was taken as three separate vertically layered sample units of one inch (25 mm.) each, making five sample units in all. Four such sets of sample units were taken at one foot (30.5 cm.) distance from two individual tree bases for each of four tree species, making a total of 160 sample units in all. The presence of stones and roots made accurate cutting of the samples difficult. As the numbers of individuals recovered per sample unit was low, the samples have been summed by mite species (table 1). *P. piger* was the most abundant species overall, and was clearly predominant in the litter. *H. magnum* was distributed similarly, whereas *O. loricata* was the commonest species in the humus layer. *H. spinosum* was so rare that no conclusions could be reached for this species.

Categories of sample unit				
	Depths in soil	Individual Trees	Tree Species	Replications
Number of sample units	5	2	4	4
				Total
				160

Table 1 Vertical distribution of the species of Phthiracarid mites at Marian y Winllan on 28/1/60. Each figure represents the total number recorded from 20 samples.

Species of mite	Litter	Humus	1 inch*)	Soil 2 inches	3 inches
<i>Phthiracarus piger</i>	69	17	—	—	—
<i>Hoplodermma magnum</i>	21	4	—	2	—
<i>Oribotritia loricata</i>	6	30	—	2	1
<i>Hoplodermma spinosum</i>	2	2	—	—	—

\*) 1 inch = 25.4 mm.

AS VAN DER DRIFT (1951) and HAARLØV (1951) have suggested, the fermentation layer may contain a large proportion of the soil animals, and the low numbers recorded from the sample units may have been due to a high mortality occurring when dividing the litter and humus layers. Consequently, the second sampling, in July 1960, was arranged differently. Sampling positions were paired; in the first set of sample units the same procedure as in the January sampling was used but only to a depth of one inch (25 mm.) in the soil; the adjacent sample unit was cut to include all the litter and half the humus in the first core, half the humus and one half inch (12.5 mm.) of soil in the second core, and one half inch of soil (12.5 mm.) in the third core. Two such pairs were taken under each of four trees of each species, making a total of 192 sample units for extraction. If the mites were most numerous at the interface between two soil layers, and if cutting the core into subsamples causes a mortality, then the totals recorded for the different sampling methods of paired sites might be expected to show a consistent difference.

This second sampling confirmed the initial observations on depth distribution (table 2): *O. loricata* however, seems to be more widely distributed and is common throughout the litter and humus layers in this summer sampling. For reasons advanced later, these data have been transformed, and the two sets of figures compared by a 't' test (table 3).

Table 2 Total numbers of mites recorded from adjacent samples cut in two different ways on 17/6/60.  
Each figure represents the total number recorded from 32 samples.

	Litter	Humus	Soil	Litter + 1/2 humus	1/2 humus + 1/2 inch soil	1/2 inch soil
<i>Abies</i>						
<i>H. magnum</i>	6	—	—	4	3	—
<i>P. piger</i>	52	26	1	33	12	2
<i>O. loricata</i>	11	6	1	11	9	—
<i>H. spinosum</i>	6	1	—	8	—	1
<i>Larix</i>						
<i>H. magnum</i>	1	4	1	2	—	—
<i>P. piger</i>	19	50	—	61	5	—
<i>O. loricata</i>	8	38	2	40	7	—
<i>H. spinosum</i>	3	2	—	5	—	—
<i>Picea</i>						
<i>H. magnum</i>	12	—	—	31	—	—
<i>P. piger</i>	75	14	—	121	1	—
<i>O. loricata</i>	27	46	—	44	26	—
<i>H. spinosum</i>	1	—	—	11	—	—
<i>Pinus</i>						
<i>H. magnum</i>	15	1	—	18	2	1
<i>P. piger</i>	36	5	—	52	3	2
<i>O. loricata</i>	30	30	—	34	42	1
<i>H. spinosum</i>	9	—	—	15	3	1

Table 3 Comparison by means of a 't' test of the total numbers of mites recorded from adjacent sets of sample units cut in two different ways

Species of mite	Total counts for Litter/humus/soil	Total counts for litter + 1/2 humus/ 1/2 humus + 1/2 inch soil/ 1/2 inch soil	't'
<i>H. magnum</i>	27.5	35.6	1.0
<i>P. piger</i>	107.7	104.6	0.1
<i>O. loricata</i>	85.3	95.4	0.1
<i>H. spinosum</i>	19.5	30.4	1.5

Note: With 6 degrees of freedom,  $t = 2.45$  for  $P = .05$

Although the totals are higher in the sampling where the cuts were made halfway through the humus and soil layers for three of the four Phthiracarid species, in no case was the value of 't' significant.

### 3.2. Degree of Aggregation

A number of workers have recently shown that many field populations of animals have a skewed distribution, suggesting a nonrandom or aggregated distribution. This has been shown to occur particularly in those groups of animals inhabiting the soil. SALT et al. (1944, 1946, 1948) on wireworms, NIELSEN (1954) and O'CONNOR (1957) on Enchytraeids, NIELSEN (1949) on Nematoda, SATCHELL (1955) on Lumbricidae, EDWARDS (1955) on Symphylidae, and more recently HARTENSTEIN (1961) on Oribatidae. Although soil mites are very common, little information exists on the pattern of their distribution. NEF (1962) has shown that sample counts are distributed asymmetrically about their

mean, suggesting that the mites have an aggregated distribution, and a similar situation has also been described by HOBART (Unpubl.).

To determine whether the Phthiracarid population at Marian y Winllan was aggregated, 80 samples were taken at random under two trees of *Pinus sylvestris*, and counts of Phthiracarid mites were made. In all four species, the distribution is skewed, showing an excess of high numbers and blanks compared with random expectation. This suggests that the populations are aggregated (GRIEG-SMITH, 1957). The variance/mean ratio or relative variance has been used as a measure of this aggregation (CLAPHAM, 1936), and all four species of mites were found to be significantly aggregated. (*H. magnum*, *H. spinosum* and *O. loricata* at the  $P = .001$  level, and *P. piger* at the  $P = .05$  level).

This examination of aggregated distribution was then extended to cover the seasonal samplings. The variance/mean ratio for each species of mite was considered, first separately, and then together. The ratios based on the totals are highly significant for all four mites, and so are the majority of values derived for each sampling date. The figures are less convincing for *H. spinosum*, but since this species was a relative rarity, too much importance should not be attached to the nonsignificant values.

### 3.3. Transformation of the Raw Data

The total counts for each of the four species of mites, plotted as standard deviations from the mean, were compared with the distributions using the square root and logarithmic transformations. There was some improvement in the shape of the curves, but the distribution was still skewed.

Several workers have fitted the negative binomial distribution to biological data of various types (BEALL, 1940, 1942, 1954; FISHER, 1941; ANSCOMBE, 1950; BLISS and FISHER, 1953; and HARTENSTEIN, 1961). Accordingly, the negative binomial expression was fitted to the figures derived from the mite collections, and since it was found that the data for all four Phthiracarid species conformed with the negative binomial model

$$x^1 = k^{-1/2} \sin h^{-1} 1/k x^{1/2} \equiv \frac{1}{k} \sin h^{-1} kx \text{ (BEALL, 1954)}$$

these data were transformed.

### 3.4. Horizontal Distribution

#### 3.4.1. Spatial Distribution

On the first two sampling dates, i. e. July and October 1959 samples were taken at the tree base, and 1 foot, 2 feet and 3 feet (31, 62 and 93 cm.) from it in the form of two transects, one up the slope and the other down from the base of the tree. A 't' test was carried out comparing the samples taken on the upper side of the tree with those on the lower side, and this showed that the differences were not significant (table 4.). For the remaining sampling dates, four trees of each species were sampled along a transect extending from the base in a downhill direction.

Table 4 Values of 't' derived from a comparison of the transformed data for the samples taken on the upper side of the tree base with those taken on the lower side of the tree base

Species of mite	<i>Abies grandis</i>		<i>Larix decidua</i>		<i>Picea sitchensis</i>		<i>Pinus sylvestris</i>	
	July 59	Oct. 59	July 59	Oct. 59	July 59	Oct. 59	July 59	Oct. 59
<i>Hoplodermis magnum</i>	0.90	0.20	0.01	0.18	0.29	0.50	0.03	0.16
<i>Phthiracarus piger</i>	0.11	0.36	0.87	0.32	0.01	0.37	0.03	0.15
<i>Oribotritia loricata</i>	0.47	1.25	0.17	0.70	0.30	0.22	0.34	0.27
<i>Hoplodermis spinosum</i>	—	0.31	—	—	—	0.41	—	—

Note: For 14 degrees of freedom,  $t = 2.15$  for  $P = .05$

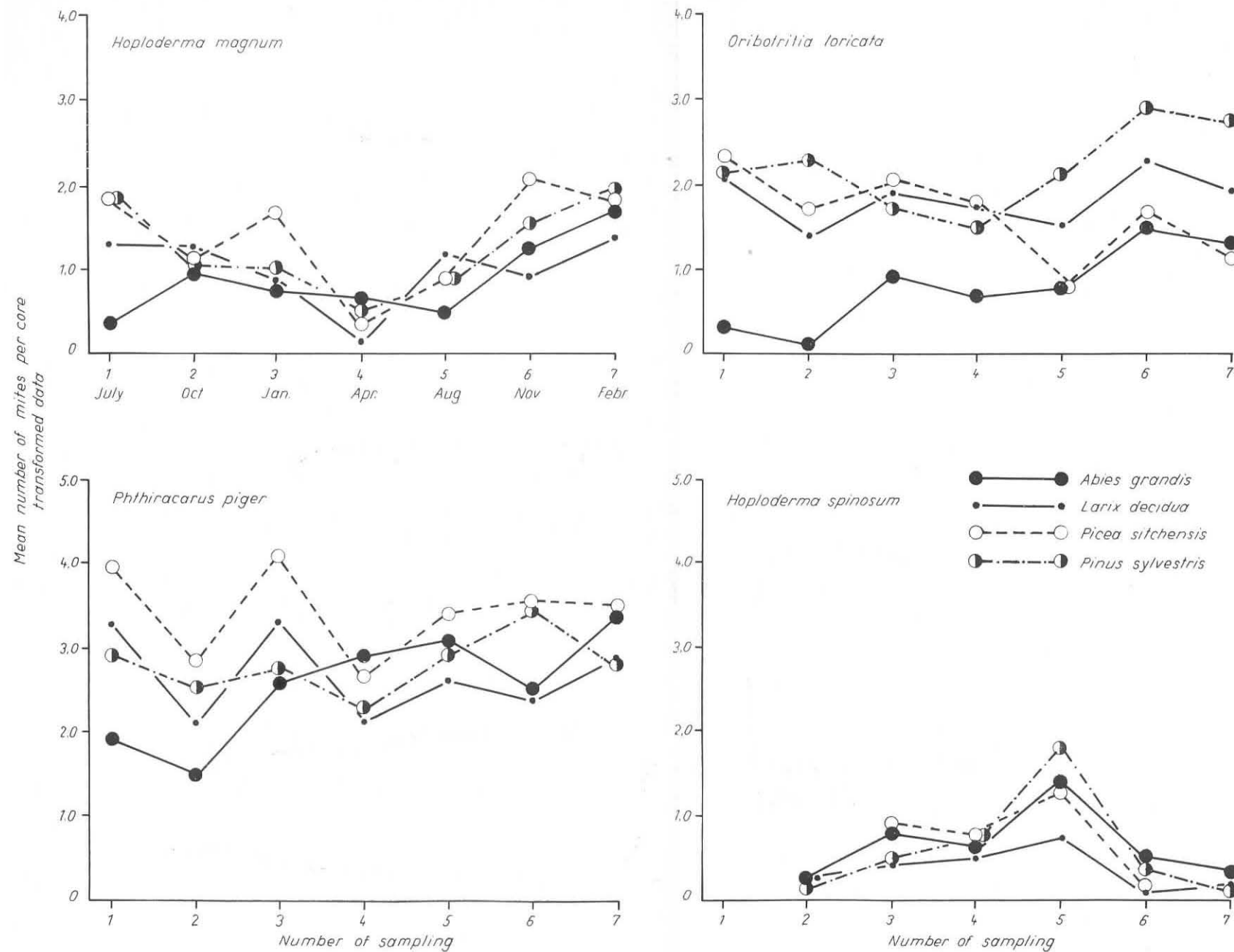


Fig. 1. Distribution of the Phthiracarid mites at Coed Marian y Winllan under different tree species. Sampling occasions are: 1. July 1959; 2. October 1959; 3. January 1960; 4. April 1960; 5. July 1960; 6. November 1960; 7. February 1961.

These data for the 7 sampling dates were analysed by a two-way analysis of variance comparing sampling positions along a transect with the complete transect. Only in the case of *H. spinosum* under *Picea* was there a significant difference at the .05 level between any two sampling points. There is, therefore, no real change in population along the length of a transect.

Significant differences between transects were more common; in the case of *H. magnum* two occasions, *P. piger* six occasions, *O. loricata* eight occasions, and *H. spinosum* one occasion out of 28. However, when the actual differences were compared, they were found to be not consistent, since the same trees did not show constant differences on successive sampling dates.

### 3.4.2. Distribution under Different Tree Species

The data for the four separate tree species have been compared for each sampling date by analysis of variance, and the results are shown in table 5. Sixteen samples were taken under each tree species and all these 64 samples have been treated to show whether significant differences exist in distribution by tree species. It is noteworthy that the

Table 5 Distribution of mites under the different tree species

Date of sampling	Variance ratio for species	
<i>Hoplodermia magnum</i>		
Jul. 59	14.25***	<i>Abies</i> sign. lower than other species
Oct. 59	0.57	
Jan. 60	3.88*	<i>Picea</i> sign. higher than <i>Abies</i> , <i>Pinus</i> , <i>Larix</i>
Apr. 60	2.09	
Aug. 60	1.89	
Nov. 60	4.85*	<i>Picea</i> sign. higher than <i>Abies</i> , <i>Larix</i>
Feb. 61	1.17	
<i>Phthiracarus piger</i>		
Jul. 59	6.09**	<i>Picea</i> sign. higher than <i>Abies</i> , <i>Larix</i>
Oct. 59	5.69**	<i>Picea</i> sign. higher than <i>Abies</i>
Jan. 60	3.07*	<i>Picea</i> sign. higher than <i>Abies</i>
Apr. 60	0.73	
Aug. 60	0.88	
Nov. 60	4.05**	<i>Picea</i> , <i>Pinus</i> sign. higher than <i>Abies</i> , <i>Larix</i>
Feb. 61	0.92	
<i>Oribotritia loricata</i>		
Jul. 59	8.82***	<i>Abies</i> sign. lower than <i>Larix</i> , <i>Picea</i> , <i>Pinus</i>
Oct. 59	8.01***	<i>Abies</i> sign. lower than <i>Larix</i> , <i>Picea</i> , <i>Pinus</i>
Jan. 60	2.26	
Apr. 60	1.97	
Aug. 60	7.32***	<i>Pinus</i> sign. higher than <i>Abies</i> , <i>Picea</i>
Nov. 60	2.38	
Feb. 61	5.39**	<i>Pinus</i> sign. higher than <i>Abies</i> , <i>Picea</i>
<i>Hoplodermia spinosum</i>		
Jul. 59	—	
Oct. 59	1.13	
Jan. 60	2.55	
Apr. 60	1.97	
Aug. 60	4.03**	<i>Larix</i> sign. lower than <i>Pinus</i>
Nov. 60	3.94**	<i>Abies</i> sign. lower than <i>Larix</i> , <i>Pinus</i>
Feb. 61	—	

compared with a second set taken in summer, but no real differences were noted in depth distribution.

The common experience of skewed data and a good fit to a negative binomial (HARTENSTEIN, 1961; NEF, 1962) was confirmed. The biological basis for this is as yet uncertain.

The various species of mites were distributed differently under each species of conifer, and there was a consistently lower population of *H. magnum*, *P. piger* and *O. loricata* under *Abies grandis*, compared with *Larix*, *Picea* and *Pinus*. Although there is as yet no direct evidence, it may well be that this low population is related partly to the size and shape of the needles, and to the manner in which they pack down on the forest floor. The long, flat needles of *Abies* tend to pack more closely, with consequently smaller interstices, than the longer, spirally twisted needles of *Pinus* on the one hand, or the short rhomboid needles of *Picea* on the other. In addition, *Abies grandis* litter tends to dry out more rapidly on the forest floor than does *Picea sitchensis* litter, which may also in part account for the differences in population. Moreover, it may well be that the looser packing of the short needles of *Picea* and the greater total thickness of the litter layer under this species, coupled with the slow rate of water loss, may account for the significantly larger populations of Phthiracarid mites found under *Picea sitchensis*.

Counts of Phthiracarid mites made at different times of year showed certain trends, but there was very considerable variation within each sampling. Since the total numbers of mites at each sampling were rather low, and since the sampling was carried out for 21 months only, it is clearly unwise to attach too much importance to the observed changes in population, and to the absence of any real annual trends.

### 5. Summary

The work described was carried out in a mixed coniferous woodland in North Wales, the tree species represented being *Abies grandis*, *Larix decidua*, *Picea sitchensis* and *Pinus sylvestris*.

Samples of the Phthiracarid populations were taken at three monthly intervals over a period of 21 months.

All species of Phthiracarid mites occurred predominantly in the litter and humus layers. Both *Hoploclerid magnum* and *Phthiracarus piger* were recorded mainly from the litter, whereas *Oribotritia loricata* occurred commonly throughout the litter and humus layers. Comparison of these layers with samples cut halfway down each layer to include the interface between two layers has shown that although the numbers for all species of Phthiracarid mites were greater in the second type of sampling, the differences were not significant.

All four species of mites had aggregated populations at all seasons of the year.

*H. magnum*, *P. piger* and *O. loricata* all showed consistently lower populations under *Abies grandis* compared with the other three tree species. On some occasions the populations under *Picea sitchensis* were significantly higher than under the other three tree species. *H. spinosum* showed no real differences in distribution by tree species.

No real seasonal differences were demonstrated for any of the four Phthiracarid species.

### 5. Zusammenfassung

Die hier beschriebene Untersuchung wurde in einem gemischten Nadelwald von Nord-Wales durchgeführt. Die Baumarten werden vertreten durch *Abies grandis*, *Larix decidua*, *Picea sitchensis* und *Pinus sylvestris*.

Während der Dauer von 21 Monaten wurden in dreimonatigem Abstand Proben des Phthiracarenbesatzes entnommen.

Alle Phthiracariden kommen hauptsächlich in der Streu und in den Humusschichten vor. *Hoploclerid magnum* und *Phthiracarus piger* wurden beide hauptsächlich in der Streu gefunden, während dagegen *Oribotritia loricata* gewöhnlich sowohl in der Streu als auch in der Humusschicht vorkommt. Der Vergleich mit Proben aus dem Grenzbereich zwischen Streu- und Humusschicht hat gezeigt, daß in diesem zwar die Individuenzahl aller Phthiracariden-Arten größer ist als in den Schichten selbst, daß aber die Differenzen nicht signifikant waren.

Alle vier Milbenarten waren zu jeder Jahreszeit in größerer Zahl vertreten.

Die Besatzdichte von *Phthiracarus piger* und *Oribotritia loricata* war unter *Abies grandis* übereinstimmend höher als unter anderen Baumarten. In einigen Fällen waren die Populationen

unter *Picea sitchensis* signifikant höher als unter anderen Baumarten. *Hoplodermia spinosum* zeigte keine von den Bäumen wesentlich beeinflussten Verteilungsunterschiede.

Von keiner der vier Phthiracariden-Arten wurde eine wirkliche jahreszeitliche Schwankung der Besatzdichte beobachtet.

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## 7. Literature

- ANSCOMBE, F. J., 1950. Sampling theory of the negative binomial and logarithmic series distributions. *Biometrika*, **37**, 358—382.
- ATALLA, E. A. R., 1961. Studies on the ecology of some selected soil mites. M.Sc. Thesis, University of Wales.
- BEALL, G., 1940. The fit and significance of contagious distributions when applied to observations on larval insects. *Ecology*, **21**, 460—474.
- BEALL, G., 1942. The transformation of data from entomological field experiments so that analysis of variance becomes applicable. *Biometrika*, **32**, 243—262.
- BEALL, G., 1954. Data in binomial or near binomial distributions. In: KEMPTHORNE et al., *Statistics and Mathematics in Biology*. Iowa State College Press.
- BLISS, C. I., and FISHER, R. A., 1953. Fitting the negative binomial distribution to biological data. *Biometrics*, **9**, 176—200.
- CLAPHAM, A. R., 1936. Overdispersion in grassland communities and the use of statistical methods in plant ecology. *J. Ecol.*, **24**, 232—251.
- CLAPHAM, A. R., TUTIN, T. G., and E. F. WARBURG, 1952. *Flora of the British Isles*, Cambridge University Press. 1st Edition.
- DIXON, H. N., 1955. The students handbook of British Mosses. Sumfield and Day, Ltd.
- DRIFT, J. VAN DER, 1951. Analysis of the animal community in a beech forest floor. *Tijdschr. Ent.*, **94**, 1—168.
- DUNGER, W., 1958. Über die Veränderung des Fallaubes im Darm von Bodentieren. *Z. Pflanzenernähr. Düngung, Bodenkunde* **82**, 174—193.
- EDWARDS, C. A. T., 1955. Soil sampling for Symphilids. *Soil Zoology* ed. D. K. McE. KEVAN. Butterworths Scientific Publications, London, 412—416.
- EVANS, G. O., 1951. Investigations on the fauna of forest humus layers, Rep. Forest Research. Forestry Commission, London. 110—113.
- FISHER, R. A., 1941. The negative binomial distribution. *Ann. Eugen. London*, **2**, 182—187.
- FORSSELL, K. H., 1938. Bidrag till konnedom om djurlivets i morken på markomvand lingen. 1. Om några hornvalsters (Oribatiders) näring. *Medd. Skogsforsöksanst. Stockh.*, **31**, 81—107.
- GRIEG-SMITH, P., 1957. *Quantitative Plant Ecology*. Butterworths Scientific Publications, London.
- HAARLOV, N., 1955. Vertical distribution of mites and Collembola in relation to soil structure. *Soil Zoology*, ed. D. K. McE. KEVAN. Butterworths Scientific Publications, London, 167—178.
- HARTENSTEIN, R., 1961. On the distribution of forest soil Arthropods and their fit to 'contagious' distribution functions. *Ecology*, **62**, 190—194.
- HAYES, A. J., 1962. Studies on the decomposition of coniferous litter with special reference to the role of Phthiracarid mites. Ph. D. Thesis, University of Wales.
- HOBART, J., Unpublished data.
- JACOT, A. P., 1936. Spruce litter reduction. *Canad. Ent.*, **68**, 31.
- JACOT, A. P., 1939. Reduction of Spruce and Fir litter by minute animals. *J. For.*, **37**, 858—860.
- MACFADYEN, A., 1953. Notes on methods for the extraction of small soil arthropods. *J. Anim. Ecol.*, **22**, 65—77.
- MURPHY, P. W., 1955. Note on the processes used in sampling, extraction and assessment of the meiofauna of heathland. *Soil Zoology*, ed. D. K. McE. KEVAN. Butterworths Scientific Publications, London. 338—340.

- NEF, L., 1962. The distribution of Acarina in the soil. Progress in Soil Zoology. ed. P. W. MURPHY. Butterworths Scientific Publications, London, 56—59.
- NIELSEN, C. OVERGAARD, 1949. Studies on the microfauna. II. The soil inhabiting nematodes. Nat. Jutland., **2**, 1—131.
- NIELSEN, C. OVERGAARD, 1954. Studies on the Enchytraeidae. III. The microdistribution of Enchytraeidae. Oikos, **5**, 167—178.
- O'CONNOR, F. B., 1957. An ecological study of the Enchytraeid worm population of a coniferous forest soil. Oikos, **8**, 162—199.
- POOLE, T. B., 1957. An ecological study of the Collembola of a coniferous forest soil. Ph. D. Thesis, University of Wales.
- POOLE, T. B., 1961. An ecological study of the Collembola of a coniferous forest soil. Pedobiologia, **1**, 113—137.
- RIHA, G., 1951. Zur Ökologie der Oribatiden in Kalksteinböden. Zool. Jb. Syst., **80**, 407—460.
- SALT, G., and HOLLICK, F. S. J., 1944. Studies of wireworm populations. I. A census of wireworms in pasture. Ann. appl. Biol., **31**, 52—64.
- SALT, G., and HOLLICK, F. S. J., 1946. Studies of wireworm populations. II. Spatial distribution. J. exp. Biol., **23**, 1—46.
- SALT, G., HOLLICK, F. S. J., RAW, F., and BRIAN, M. V., 1948. The Arthropod population of pasture soil. J. Anim. Ecol., **17**, 139—150.
- SATCHELL, J. E., 1955. Some aspects of earthworm ecology. Soil Zoology. ed. D. K. McE. KEVAN. Butterworths Scientific Publications, London.
- SCHUSTER, R., 1955. Untersuchungen über die bodenbiologische Bedeutung der Oribatiden. Naturwissenschaften, **42**, 108.
- SCHUSTER, R., 1956. Der Anteil der Oribatiden an den Zersetzungs Vorgängen im Boden. Z. Morph. Ökol. Tiere, **45**, 1—33.
- SPENCER, J. A., 1951. The role of Acarina in the decomposition of forest litter. Special subject report. Unpublished. Department of Forestry, University of Oxford.
- TURK, F. A., 1953a. A synonymic Catalogue of British Acari. Part 1. Ann. and Mag. Nat. Hist. (12th Series), **6**, 1—26.
- TURK, F. A., 1953b. A synonymic Catalogue of British Acari. Part 2. Ann. and Mag. Nat. Hist. (12th Series), **6**, 81—99.
- WALLWORK, J. A., 1958. Notes on the feeding behaviour of some forest soil Acarina. Oikos, **9**, 260—271.
- WATSON, E. V., 1955. British Mosses and Liverworts. Cambridge University Press.
- WILLMANN, C., 1931. Moosmilben oder Oribatiden. In Dahls Tierwelt Deutschlands. Bd. **22**, 79—200.
- WOODRING, J. P., and COOKE, E. F., 1962. The biology of *Ceratozetes cisalpinus* BERLESE, *Scheloribates laevigatus* KOCH, and *Oppia neerlandica* OUDEMANS (Oribatei) with a description of all stages. Acarologia, **4**, 101—137.

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